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# Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing

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ABSTRACT

Annual fecundity has been increasingly advanced as a preferred measure of stock reproductive potential (*SRP*), yet estimates are methodologically challenging, particularly for species with indeterminate fecundity. Inherent variability due to energetic and environmental constraints increases the uncertainty of annual fecundity estimates, and this uncertainty may have important consequences for management guidance. In this study, we assessed how size-dependent reproductive timing interacts with age truncation to impact estimates of *SRP* in spotted seatrout (*Cynoscion nebulosus*), using a combination of modeling techniques. Positive size dependence in spawning frequency, or the number of spawning events in a season, had a substantial impact on both the *SRP* and estimates of stock status relative to management targets. The loss of the oldest age classes, even under relatively low fishing pressures, resulted in a significant decline in *SRP* due to the disproportionately large contribution by these age classes. Not surprisingly, the effect increased with the strength of the size-dependent relationship, which also resulted in reducing the proportionality between *SRP* and spawning stock biomass (*SSB*). The potential for erroneously classifying the health of a stock was amplified when the population approached the management target because of the uncertainty and inherent variability in *SRP*. For management, characterizing all of the size-dependent relationships with *SRP* (batch fecundity, reproductive timing, egg/larval quality) may be more critical than obtaining precise estimates of *SRP* when management reference points are relative to unexploited conditions, as in spawning potential ratios (*SPRs*).

## 1. Introduction

Reproductive traits (e.g., timing, location, egg and larval quality) can drive the productivity of a stock (Murawski et al., 2001; Berkeley et al., 2004a; Lowerre-Barbieri et al., 2011a), and these traits are often influenced by demographic changes (Wright and Trippel, 2009). Older age classes, even at relatively low abundances, can produce the majority of eggs in a population (Mehault et al., 2010) through positive size relationships with fecundity (Marteinsdottir and Begg, 2002; Murua et al., 2006; Thorsen et al., 2010), reproductive timing (Parrish et al., 1986; Claramunt et al., 2007; LaPlante and Schultz, 2007; Lowerre-Barbieri et al., 2011b; Fitzhugh et al., 2012), and egg quality (Murawski et al., 2001; Scott et al., 2006). Consequently, age truncation due to increasing fishing pressure can lead to disproportionately large declines in egg production as these older age classes are removed (Berkeley et al., 2004a; Wright and Trippel, 2009). Due to these size- and age-dependent effects, spawning stock biomass (*SSB*) is often not proportional to stock reproductive potential (*SRP*; Trippel, 1999), despite its continued use as a primary metric in stock-recruitment relationships (Marshall, 2009) and in estimating the status of a stock for management guidance. As such, traditional stock assessments based on *SSB* can underestimate the impacts of age truncation and overestimate stock reproductive potential (Trippel, 1999; Murawski et al., 2001; Marshall, 2009), and multiple authors have suggested that population annual fecundity (or total egg production, *TEP*) provides a more appropriate index of *SRP* than *SSB* (Marshall et al., 1998; Morgan et al., 2009; Mehault et al., 2010).

In fishes with indeterminate fecundity, unyolked oocytes are continuously recruited and spawned in batches, and the product of batch fecundity and the number of spawns per season provides an estimate of annual fecundity (Hunter et al., 1985). Determining the total number of spawns per season, defined as the spawning frequency of a population (Lowerre-Barbieri et al., 2011b), is methodologically challenging. The spawning frequency is equal to the product of the spawning interval between consecutive spawns and the spawning season duration, where the spawning interval is traditionally calculated as the reciprocal of the proportion of active spawners (Hunter and Macewicz, 1985). However, this approach assumes that no migration among sampling areas occurs during the spawning season, which may be inaccurate for many species

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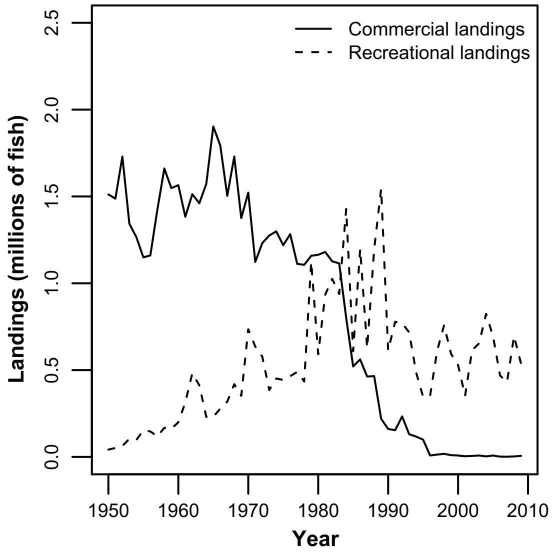

**Fig. 1.** Estimated annual *C. nebulosus* landings (number of fish) for the commercial and recreational fisheries within the Southwest region of Florida during 1950–2009 (adapted from Murphy et al., 2011).

(Lowerre-Barbieri et al., 2009; Ganias, 2011). Because oocytes are continuously recruited and spawned, the annual fecundity of these species is not limited by body cavity size (Sadovy, 1996), but instead by energetics (Hunter and Leong, 1981; Pecquerie et al., 2009) and the environment (Curtis, 2007; Ganias, 2009). Although individual variability in spawning frequency is often not assessed, a few studies have found variable spawning intervals over the season and by sex (Asoh, 2003; Curtis, 2007; Patzner, 2008). Failure to account for this variability can impact estimates of annual fecundity and management decisions (Lowerre-Barbieri et al., 2011b).

The purpose of this study was to assess the impacts of age truncation and size-dependent reproductive timing on *SRP* for a species with indeterminate fecundity. We chose spotted seatrout, *Cynoscion nebulosus*, as our model species for this analysis due to the extensive data available for this species (Lowerre-Barbieri et al., 2009; Murphy et al., 2011) and its periodic life-history strategy, which is representative of most recreationally and commercially targeted species (Winemiller, 2005). *C. nebulosus* is a highly fecund, multiple-batch spawner (Brown-Peterson, 2003) with observed maximum ages of 5–9 years in exploited populations but known to live up to 12 years (Maceina et al., 1987; Nieland et al., 2002). Historically, this species was heavily exploited by commercial fisheries in Florida, but the fishery has shifted to primarily recreational since the 1980s (Fig. 1). Currently *C. nebulosus* is the most targeted sport fish in the Gulf of Mexico (National Marine Fisheries Service, 2007), where they exhibit substantial age truncation. The specific objectives of this study were two-fold: (1) to assess the relative contribution of the oldest age classes to *SRP* across a range of fishing pressures and size-dependent spawning relationships; and (2) to determine if uncertainty in the size dependence of spawning substantially impacts the perception of stock health. Using a combination of modeling techniques, we assessed how statistical uncertainty in the relationship between fish length and the daily probability of spawning interacts with variable age truncation to impact estimates of *SRP*. This approach and results should be applicable to many batch spawners with indeterminate fecundity whose spawning frequency is influenced by an individual's state and the environment, and where size dependence with spawning frequency is likely to exist.

## 2. Materials and methods

### 2.1. Overview

We developed a series of linked models (Fig. 2) to estimate stock reproductive potential under alternative size-dependent spawning frequency scenarios, for a range of fishing pressures and resultant degrees of age truncation. We first developed a statistical model (generalized additive model, *GAM*) to estimate the probability of spawning as a function of date, length, and spatial zone. This model provided a range of statistical uncertainty for the various predictors, and we used the uncertainty in the size predictor effect as a potential range of size-dependent relationships with spawning frequency (none, average, and upper and lower confidence levels of the functional relationship; see below for more detail). An individual based model (*IBM*) was linked to the *GAM* to predict individual growth trajectories, size at maturity, and annual fecundity per fish under the alternative size-dependent spawning relationships. The estimates of total egg production (*TEP*) produced by these two models were then used as inputs into a statistical catch-at-age model (*SCAM*) to derive estimates of *SRP* across a historical time frame with variable fishing pressures. All model analyses presented herein are based on *C. nebulosus* in southwest Florida waters, utilizing reproductive data from Lowerre-Barbieri et al. (2009; see therein for a description of data collection) and the *SCAM* from the current stock assessment for this species (Murphy et al., 2011; see therein for a description of the data sources and model structure).

### 2.2. Probability of spawning

The probability of female spawning was modeled using a *GAM* (e.g. Kupschus, 2004) and data on the incidence of active spawners within the spawning population (Fig. 3). These data were collected over a range of time (diel and seasonal), size/age, and space (Lowerre-Barbieri et al., 2009). The *GAM* used the same predictor variables (date, length, and spatial zone) as those used in the

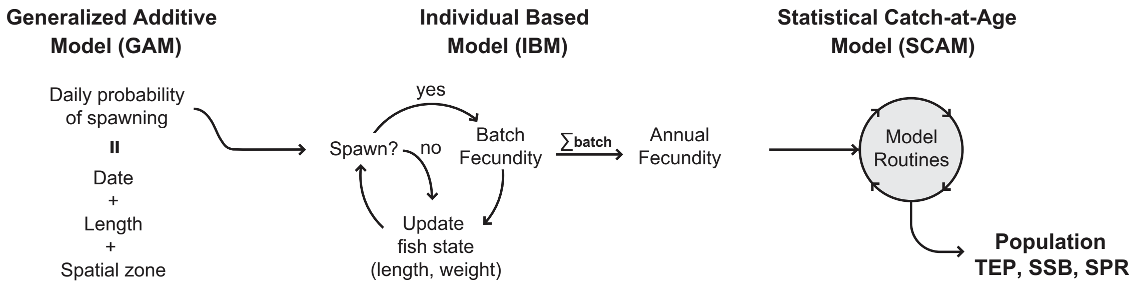

**Fig. 2.** Schematic of the overall modeling approach used to estimate stock reproductive potential, showing the linkages between the three models used in this study. The *GAM* estimated the daily probability of spawning based on field data, and this probability determined if spawning occurred for each fish in the *IBM* on a daily time step. The age-specific annual fecundity estimates were then used by the *SCAM* to derive annual estimates of the population's total egg production (*TEP*), spawning stock biomass (*SSB*), and spawning potential ratio (*SPR*).

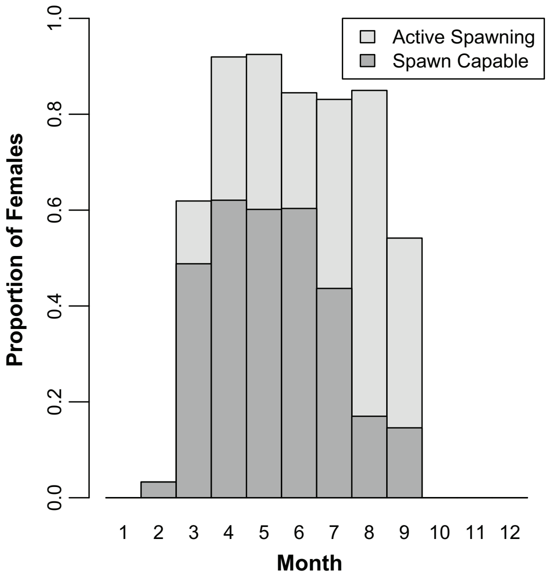

**Fig. 3.** Proportion of *C. nebulosus* females in the spawning capable and active spawning sub-phases (adapted from Lowerre-Barbieri et al., 2009, Fig. 4). The combined proportion (i.e., total height of the bar) represents the proportion of females in the spawning population.

generalized linear models from Lowerre-Barbieri et al. (2009), but relaxed the assumption of linearity in the predictors to explore non-linear relationships between the probability of spawning and the length and date predictors. Spatial zone was included in the model as a categorical predictor to account for spatial variability in spawning frequency, but was not directly assessed as a factor affecting reproductive potential in this study. Therefore, spawning probabilities in the *IBM* were calculated using an averaged value across all spatial zones. In addition, the inlet zone (see Lowerre-Barbieri et al., 2009) was removed from the analyses since it represented an aggregation site used exclusively for spawning. Removal of this site from the analyses did not significantly alter the shape or magnitude of the predictor effects, but did remove potential sampling biases of using aggregation-exclusive sites for calculating spawning frequencies (Ganias, 2011). In order to estimate the probability of spawning on a daily time step in the *IBM*, it was necessary to use the same time scale to identify spawners. Thus, spawners were considered those individuals sampled at night in the active sub-phase (spawning within ±2 h) or sampled in the morning in the recently spawned sub-phase (postovulatory follicles, POFs < 12 h). For each fish, the probability of spawning, conditional on being mature $p(S|M)$, was calculated using the *GAM* form:

$$p(S|M)=\frac{\exp(\beta_{s0}+\sum_l f_l(x_l))}{1+\exp(\beta_{s0}+\sum_l f_l(x_l))} \tag{1}$$

where $\beta_{s0}$ is the spawning intercept, and $f_l(x_l)$ is a function of the $l$th predictor variable $x_l$. The $f_l(x_l)$ function can take multiple forms (linear, categorical, or non-linear smoothing function), where the smoothing function is often represented as $s(x_l)$ (hereafter used in this manuscript, e.g., $s$(Length) referring to the length predictor smoothing function). The *GAM* was fit using the mgcv package (Wood, 2011) in R 2.13 (R Development Core Team, 2011). The length and day-of-year predictors were fit using penalized thin plate regression splines to automatically select the degrees of freedom for each smoothing function, with an unbiased risk estimator as the model selection criterion. Use of alternative selection criteria had a minimal effect on the predicted model.

### 2.3. Annual fecundity

To estimate the annual fecundity per fish, an *IBM* was developed that simulated growth, maturity, and, linked with the *GAM*, the probability of spawning and subsequent batch fecundity for each fish at a daily time step for a single year (see Table 1 for a list of model parameters). Natural and fishing mortality were not simulated in the *IBM*, but were accounted for explicitly in the model used to estimate stock reproductive potential (*SCAM*; see below). An individual-based approach was chosen to mimic natural variability in *SRP*, where individual variability is common in reproductive timing parameters (time of maturity, spawning period, and spawning interval), and these are often correlated with individual size (Lowerre-Barbieri et al., 1998, 2011b; Wright and Trippel, 2009). In our model, each individual had a unique state based on a combination of length, weight, and age, which affected its probability of spawning and thus simulated intra-seasonal variability in annual fecundity. Because the purpose of the *IBM* was to estimate the annual fecundity per fish in the absence of mortality, each simulation was initialized at a constant number of individuals (1 million), with a uniform age frequency distribution on January 1st, and only females were modeled.

Each fish was assigned a specific birth date since birth date can impact growth and thus survivorship and egg production (Lowerre-Barbieri et al., 1998). Birth dates were assigned in a three-step process. First, each fish was assigned an age from a random uniform distribution (0–12 year), thus determining the year it was born. Second, a birth month within the spawning season was assigned using a discrete empirical distribution (Walker, 1977) based on the proportion of individuals in the spawning population in each month of the year (Fig. 3). Third, a random day was chosen uniformly from within each month to assign an exact birth date, giving each fish a unique age in days. Once a birth date had been assigned, the length $L_{i,t}$ of the $i$th fish at age $t$ was assigned using a growth model that accommodates ontogenic changes in growth rates (Porch et al., 2002):

$$L_{i,t}=L_\infty(1-\mathrm{e}^{\beta_1+\beta_2-k_0(t-t_0)}) \tag{2a}$$

where

$$\beta_1=\frac{k_1}{\lambda_1}(\mathrm{e}^{-\lambda_1 t}-\mathrm{e}^{-\lambda_1 t_0}) \tag{2b}$$

$$\beta_2=\frac{k_2}{4\pi^2+(\lambda_2)^2}\left[\begin{array}{l}\mathrm{e}^{-\lambda_2 t}\begin{pmatrix}2\pi\cos\{2\pi(t_c-t)\}-\\ \lambda_2\sin\{2\pi(t_c-t)\}\end{pmatrix}-\\ \mathrm{e}^{-\lambda_2 t_0}\begin{pmatrix}2\pi\cos\{2\pi(t_c-t_0)\}-\\ \lambda_2\sin\{2\pi(t_c-t_0)\}\end{pmatrix}\end{array}\right] \tag{2c}$$

and

$$k_0+k_1\mathrm{e}^{-\lambda_1 t}+k_2\mathrm{e}^{-\lambda_2 t}\sin(2\pi(t-t_c))\geq 0 \tag{2d}$$

The constraint (Eq. (2d)) implies that animals will not shrink with age. The parameters in the growth model were estimated with maximum likelihood (normally-distributed error) using a combined dataset of juveniles (digitized from Fig. 7 in McMichael and Peters, 1989) and adults age-1 or older (Lowerre-Barbieri et al., 2009). Adult fish age classes were converted to an age in days by taking the difference between the date they were sampled and their assumed birth date in the aging procedure (January 1st). The $\beta_2$ component of this growth model is typically used to accommodate seasonal changes in growth rates, although a seasonal component was not detected for these data. However, the seasonal component was retained in the model because it improved the fit to the juvenile data and the overall stability of the solution compared to the damped version where $\beta_2 = 0$ (i.e., ontogenic changes only). To account for individual variability in growth (e.g., due to resource

**Table 1**
Parameter values used in the *IBM*.

| Parameter | Equation | Description | Value |
|---|---|---|---|
| $\beta_{s0}$ | 1 | Intercept for the probability of spawning *GAM* | −4.7882 |
| $f$(day of year) | 1 | Spline smoothing function for the day of year predictor of the probability of spawning *GAM*; also represented as s(Day Of Year) in Fig. 4 to denote as a smoothing term | Fig. 4a |
| $f$(length) | 1 | Spline smoothing function for the length predictor of the probability of spawning *GAM*; also represented as s(Length) in Fig. 4 to denote as a smoothing term | Fig. 4b |
| $f$(zone) | 1 | Average partial effect value for the spatial zone predictor of the probability of spawning *GAM* | −0.24425 |
| $L_\infty$ | 2,3 | Growth model (Porch et al., 2002) asymptotic length (TL) | 73.85 cm |
| $L_{\infty \text{SD}}$ | 3 | Growth model asymptotic length standard deviation | 10.18 cm |
| $k_0$ | 2 | Growth model instantaneous growth rate coefficient | 0.1379 |
| $k_1$ | 2 | Growth model instantaneous growth rate coefficient | 2.6071 |
| $k_2$ | 2 | Growth model instantaneous growth rate coefficient | 4.9348 |
| $t_0$ | 2 | Growth model age intercept parameter | 0.0829 |
| $t_c$ | 2 | Growth model sine wave shifting parameter | 0.5249 |
| $\lambda_1$ | 2 | Growth model damping coefficient | 2.6998 |
| $\lambda_2$ | 2 | Growth model damping coefficient | 5.6102 |
| $a$ | 4 | Allometric length–weight scale | 0.0112 |
| $b$ | 4 | Allometric length–weight exponent | 2.9360 |
| $L_{\text{mat50}}$ | 5 | Size at 50% maturity (TL) | 26.15 cm |
| $L_{\text{matSD}}$ | 5 | Standard deviation for size at 50% maturity | 1.29 cm |
| $\beta_{f0}$ | 6 | Intercept for the batch fecundity relationship | −43139 |
| $\beta_{f1}$ | 6 | Coefficient of the weight predictor for the batch fecundity relationship | 669.6 |

availability; Lorenzen and Enberg, 2002), each fish was assigned a normally-distributed random asymptotic length at the initiation of the simulation:

$$L_{\infty,i} \sim \text{Normal}(L_\infty, L_{\infty \text{SD}}) \tag{3}$$

The standard deviation in the asymptotic length $L_{\infty \text{SD}}$ was obtained from the maximum likelihood estimate of the growth model. Once length was assigned to each fish in the simulation, the weight $W_{i,t}$ of the $i$th fish at age $t$ was assigned using the standard allometric relationship:

$$W_{i,t} = a \times L_{i,t}^{b} \tag{4}$$

Each fish was assigned a random length at maturity $L_{\text{mat},i}$ at the initiation of the model from a logistic distribution with mean length at 50% mature $L_{\text{mat50}}$ and standard deviation $L_{\text{matSD}}$:

$$L_{\text{mat},i} \sim \text{Logistic}(L_{\text{mat50}}, L_{\text{matSD}}) \tag{5a}$$

$L_{\text{mat50}}$ and $L_{\text{matSD}}$ were calculated using maximum likelihood where the proportion of mature fish $P_{\text{mat}}$ at length $L$ was modeled using the logistic function:

$$P_{\text{mat}} = \frac{1}{1 + e^{-((L - L_{\text{mat50}})/L_{\text{matSD}})}} \tag{5b}$$

After the population was initialized (i.e., all fish assigned an age, length, weight, and length at maturity), the model processes (growth, maturity, probability of spawning, and batch fecundity) were applied to each individual fish for each day of a single year, starting January 1st. Growth in length throughout the year was modeled using Eq. (2). If the fish grew larger than its assigned length at maturity (Eq. (5a)), the fish was considered mature. For each mature fish, the probability of spawning per day ($p(S|M)$, Eq. (1)) was calculated from the *GAM* based on the fish length and day of the year. If an individual spawned (i.e., a uniform random deviate was less than the probability of spawning), the batch fecundity $F_{\text{batch}}$ was calculated using a linear relationship with weight $W_{i,t}$ (Lowerre-Barbieri et al., 2009):

$$F_{\text{batch}} = \beta_{f0} + \beta_{f1} \times W_{i,L} \tag{6}$$

The batch fecundity was then summed over the number of spawning events throughout the year for each age class, providing an age-specific estimate of annual fecundity for each model run, which accounted for individual variability in size at age.

### 2.4. *IBM spawning scenarios*

The underlying relationship between size and spawning frequency is difficult to characterize in batch spawners due to methodological challenges (Ganias, 2011), although a relationship is known to exist (Lowerre-Barbieri et al., 2009) and is impacted by individual variability in spawning periods and spawning interval (i.e., time between spawns). To assess the uncertainty in the relationship between size and spawning frequency, the *IBM* was run with four alternative size-dependent spawning functional relationships (i.e., alternative representations of $s$(Length) in Eq. (1); reflecting none, weak, average, and strong relationships). These alternative size-dependent spawning relationships represented the statistical range of uncertainty estimated by the *GAM* for the length predictor, where the length predictor smoothing function ($s$(Length), Fig. 4b) provided an estimate of the underlying relationship between size and spawning frequency. The average size-dependent relationship was that estimated by the *GAM* (solid line, Fig. 4b), while the weak and strong size dependencies represented the confidence bounds (grey shaded regions, Fig. 4b). The last size-dependent spawning relationship was that of no size dependence other than with batch fecundity (dotted line, Fig. 4b). This relationship represents what has been typically assumed in fisheries science (Lowerre-Barbieri, 2009).

### 2.5. *Stock reproductive potential*

To integrate these results into a management framework, the age-specific annual fecundities, maturity-at-age, and weight-at-age estimates from the *IBM* were input into the stock assessment model used for *C. nebulosus* in Florida waters (statistical catch-at-age model, *SCAM*). The maturity- and weight-at-age estimates were obtained by taking the averages of all fish within an age class at the midpoint of the spawning season. The *SCAM* used here is representative of common statistical catch-at-age models (Fournier and Archibald, 1982), providing estimates of relative abundances per age class given proportional catch-at-age data. The *SCAM* was developed using AD Model Builder (Fournier et al., 2012), and its structure and data sources are described in the previous *C. nebulosus* stock assessments (Murphy et al., 2011). Other than fecundity-, maturity-, and weight-at-age, the data sources for the *SCAM* remained the same as in Murphy et al. (2011).

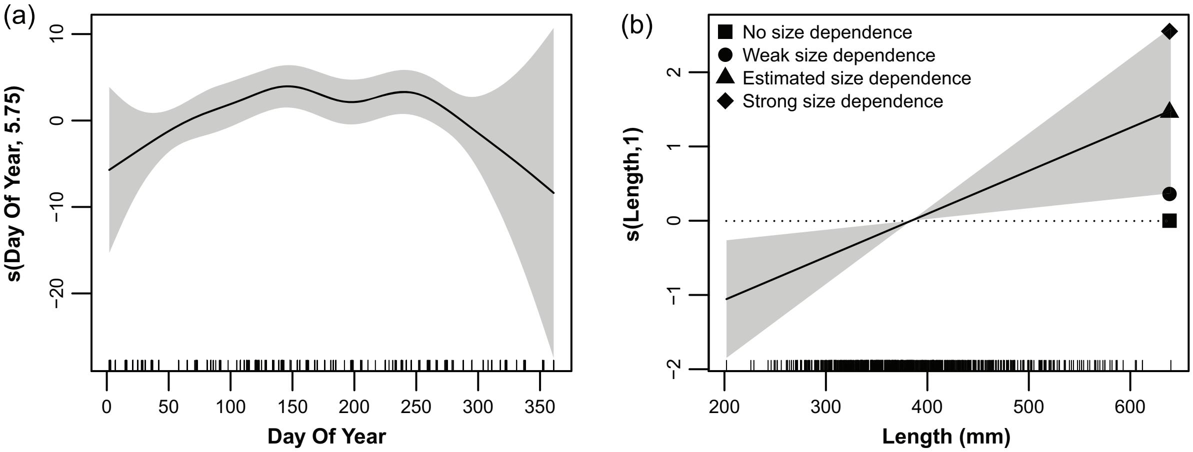

**Fig. 4.** Estimated functions for the (a) date and (b) length predictors in the generalized additive model (*GAM*) describing the probability of a fish actively spawning. The solid lines represent the best-fit estimates, the grey shaded regions represent the confidence intervals, and the dotted line in panel (b) represents the hypothetical condition with no size dependence. The four functional relationships between length and the probability of spawning used as alternative scenarios in the model analyses are marked with symbols on their corresponding linear functions in panel (b). The numbers in the *y*-axis labels represent the estimated degrees of freedom, and the tick marks along the *x*-axis represent all samples taken, including both spawning and non-spawning individuals.

Several measures of *SRP* were output from the *SCAM* to compare the alternative size-dependent spawning relationships, including: *TEP* (here considered as the annual fecundity of the population), female *SSB*, and spawning potential ratio (*SPR*). *SPR* is the biological reference point used to manage this species in Florida (target of 35% *SPR*) and is the ratio of estimated *SRP* per recruit under current fishing to that with no fishing, where the reciprocal theoretically represents the amount the stock must compensate to sustain a given yield (Lowerre-Barbieri, 2009). Because a maximum age was not explicitly modeled in the *SCAM*, it was possible for fish to survive past 12 years of age under low exploitation rates, and these older age classes were combined into an age-12 plus group.

## 3. Results

### 3.1. Probability of spawning

The *GAM* model provided an estimate of the probability of an individual actively spawning as a function of multiple predictor variables. The date and length predictors were both significant ($p < 0.01$) in the *GAM*, and the functional relationships and parameter values are presented in Fig. 4 and Table 1, respectively. For the date predictor, the probability of actively spawning peaked in both early June and late August, and decreased at the tails of the spawning season in March and late September (Fig. 4a), similar to the observed proportion of females in the spawning population

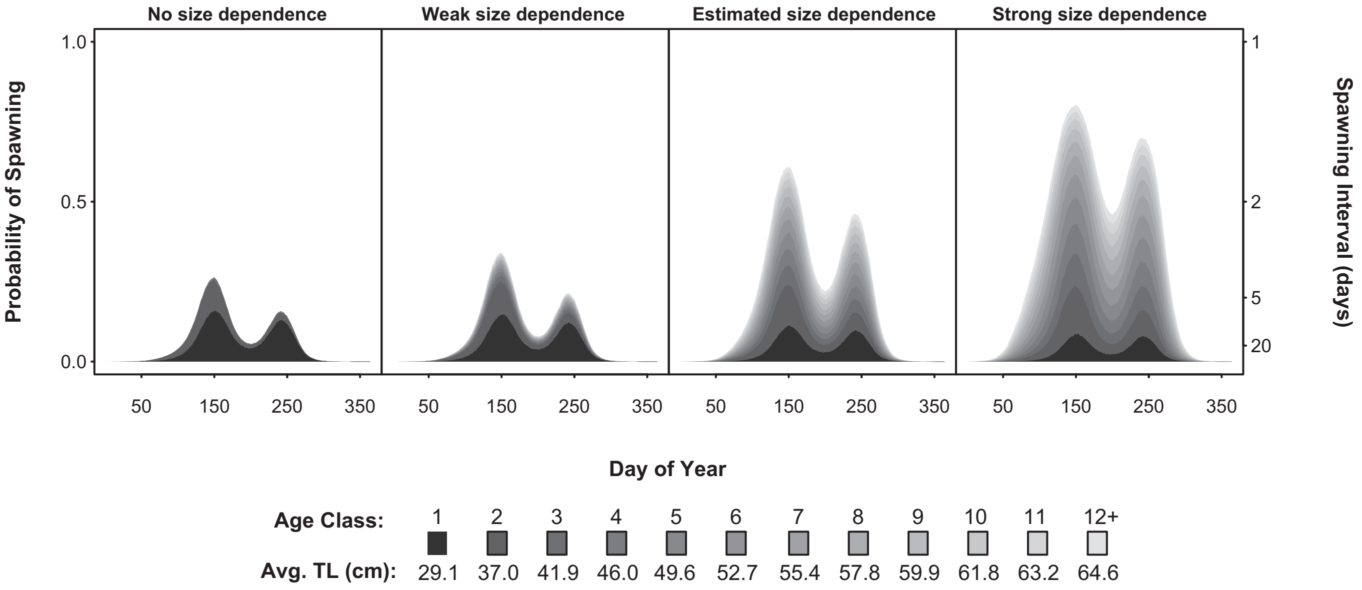

**Fig. 5.** Daily probability of spawning (left *y*-axis) and the corresponding spawning interval (right *y*-axis) for the alternative size-dependent spawning scenarios (columns). The different shades in color represent the age classes and the corresponding average total length (TL, cm) at the midpoint of the spawning season (see legend). The size dependence increases from left (none) to right (strong) in the panels. Here, the daily probability of spawning is equivalent to the spawning fraction, and the spawning interval is the reciprocal of the spawning fraction. This daily probability of spawning represents the probability of spawning conditional on being mature (Eq. (1)) times the probability of being mature: $P(S) = P(S|M)^{*}P(M)$.

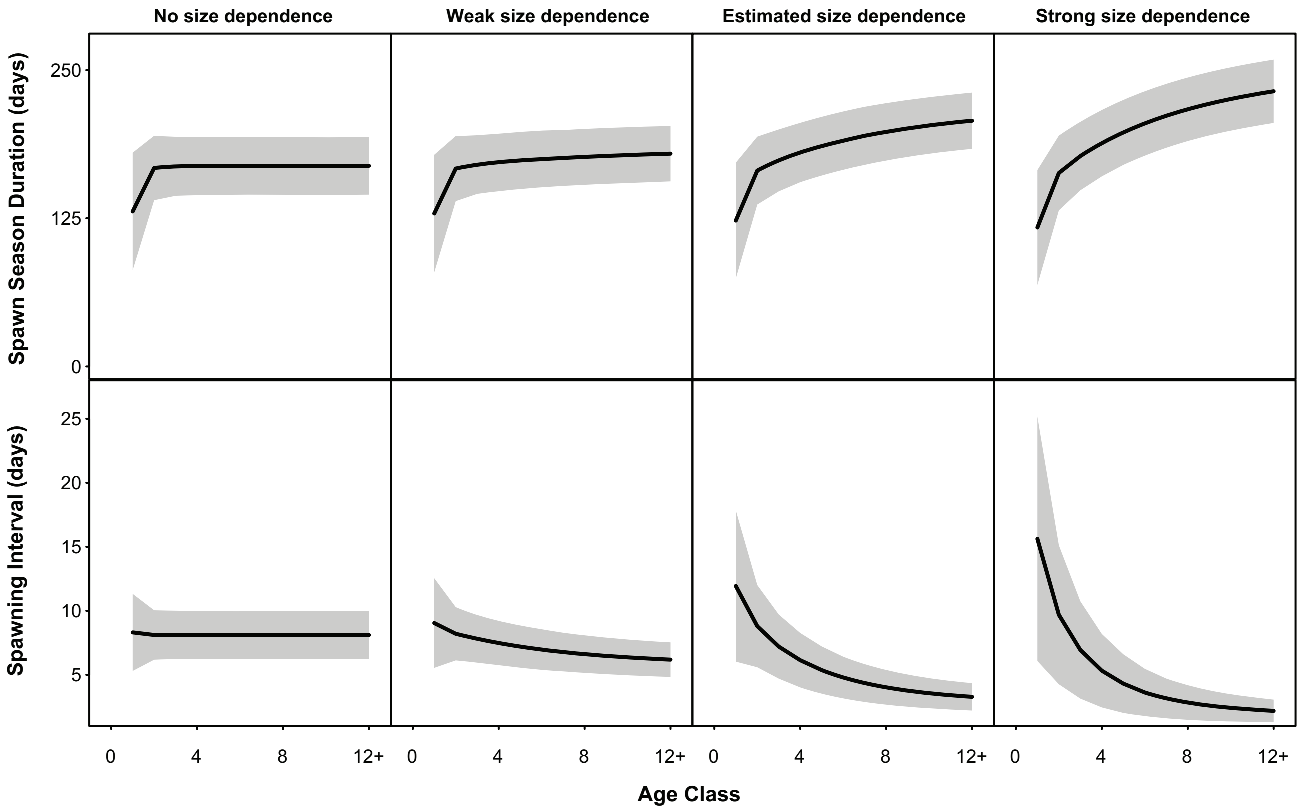

**Fig. 6.** Spawning season duration (top row) and spawning interval (bottom row) per age class for the alternative size-dependent spawning scenarios (columns). Here, the season length is calculated as the average span of days between the first and last day of spawning for each individual, and the spawning interval is the average length between consecutive spawns. The solid lines are the mean values, and the shaded regions represent the standard deviations due to individual variability. The steep change in the values between age-1 and age-2 represents maturation during the spawning season for age-1 individuals.

per month (Fig. 3). The relationship between length and the probability of spawning was estimated to be linear (Fig. 4b), where the probability of spawning, and subsequently the spawning frequency, increased with fish size.

### 3.2. Annual fecundity

Incorporating the *GAM* into the *IBM* to drive individual spawning produced unique spawning probability functions per age class for the different size-dependent spawning scenarios (Fig. 5). All age classes had the strongest peak in spawning in early June with a weaker peak in late August, although this June peak was less pronounced in age-1 individuals recruiting to the spawning population (i.e., maturing) within the spawning season. This bimodality across all age classes resulted from the shape of the *GAM* date predictor (Fig. 4a). The probability of spawning was equivalent to the spawning fraction per age class, and therefore proportional to the spawning frequency, where both the spawning season increased and the interval between spawns decreased as fish grew larger (Fig. 6). As the strength of the size-dependent spawning frequency increased, the maximum age-specific *TEP* per fish increased (Fig. 7). For the scenario where spawning frequency was not affected by size (the lower line with square end point in Fig. 7), the increase in *TEP* as fish aged was due to when fish matured and the relationship between batch fecundity and weight, similar to that observed in total spawners with determinate fecundity. The difference between the bottom line and those above it represents the potential effect of size-dependent reproductive timing on *TEP*.

### 3.3. Stock reproductive potential

Estimates of the population *TEP* were not directly proportional to *SSB* over the time span assessed (1950–2009) and were greatly affected by the underlying size-dependent spawning relationship and age truncation (Fig. 8). The discrepancy between *SSB* and *TEP* was most obvious at lower levels of fishing (*F*), when greater number of older, larger females were in the spawning population.

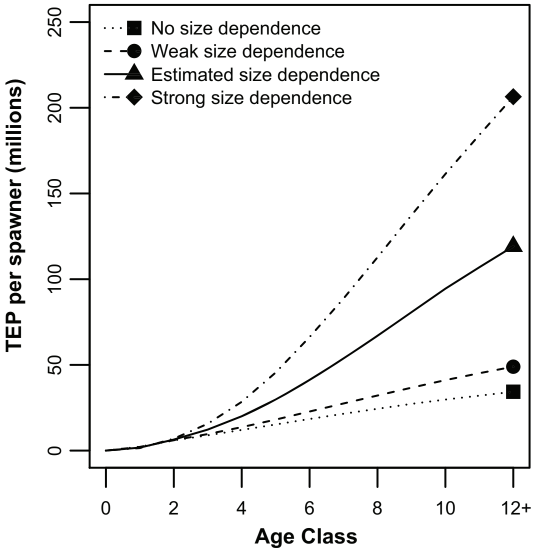

**Fig. 7.** Annual fecundity per age class for the alternative size-dependent spawning scenarios. These values represent the maximum fecundity per fish if a fish survives to the end of the spawning season.

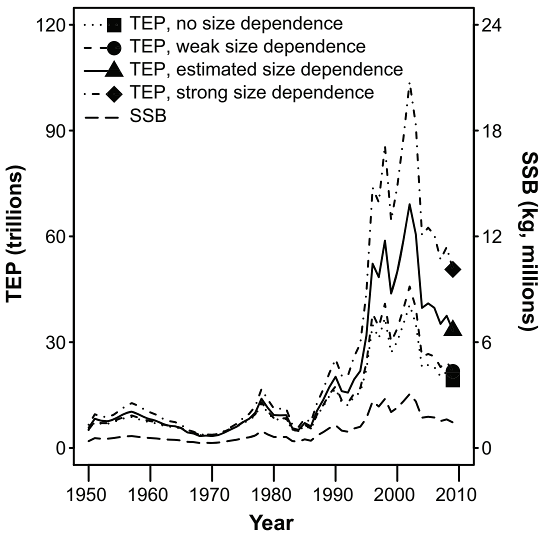

**Fig. 8.** The population annual fecundity (left *y*-axis) and female *SSB* (right *y*-axis) from 1950–2009 for the alternative size-dependent spawning scenarios. The *SSB* estimates varied little among the alternative spawning scenario model runs, so only the average of the estimates is presented.

Similarly, at these lower levels of *F*, the strong effect of the size-dependent spawning relationship was more apparent. For example during the peak of *TEP* in 2002, the difference in *TEP* estimates due to uncertainty in size dependence (i.e., strong minus weak size dependence) was 58 trillion eggs, comparable in magnitude to the range in *TEP* due to extremes in fishing pressure (66 trillion egg difference between the highest and lowest *TEP* years for the estimated size-dependent spawning relationship; Fig. 8). Comparing age distributions and their contribution to *TEP* and *SSB* at different fishing pressures (those for 1970, 2009, and no fishing, Fig. 9), *SSB* corresponded more closely to abundance than *TEP*, whereas older individuals contributed disproportionately more to the *TEP* (Fig. 9). In a virgin unfished population, older individuals (age-6+) made up 13% of the total population abundance but contributed 70% of the *TEP* for the expected size-dependent relationship. Given the estimated high abundance of the 12+ group and subsequent contribution to *SSB* and *TEP* under a virgin population (Fig. 9), it is difficult to assess if this is biologically appropriate for *C. nebulosus*, but it does highlight the potentially large magnitude of the age truncation effect. At the 2009 fishing pressure (average *F* across age classes = 0.16), the contribution of the 12+ group decreased by 88% relative to a virgin population. In comparison, at the 1970 fishing pressure (avg. *F* = 1.67), few fish survived past age-3, and the total *TEP* across all age classes was reduced to 3.3% of the virgin population ($SPR_{TEP,1970} = 0.033$; Figs. 8–10).

The *TEP*-based *SPR*s ranged from 5–14% less than the *SSB*-based *SPR*s across all years and size-dependent spawning relationships (Fig. 10). Variability in the *SPR*s due to uncertainty in size dependence was 7.9% on average across all years (grey shaded region in Fig. 10), with a minimum of 4.3% in 1970 and a maximum of 11.8% in 1996. As the fishing pressure decreased in the mid 1990s and the *SPR* of the population approached the 35% management target from 2000-present, the potential of incorrectly perceiving the population as healthy versus overfished, with respect to the target level, increased substantially. If one assumes the *TEP*-based *SPR* at the estimated size dependence is the most accurate estimate of the true reproductive potential (solid black line in Fig. 10), the *SSB*-based *SPR* would incorrectly perceive the population as above target from 1995 through 2000, while the *TEP*-based *SPR* at the strong size dependence scenario would incorrectly perceive the population as below target for eight of the nine years between 2001 and 2009. The relationship between the *TEP*- and *SSB*-based *SPR* estimates was dependent on the size-to-spawning frequency relationship, signifying an increasing disproportionality between the two as the size dependence increased (Fig. 11). This increasing disproportionality corresponds to the additional loss of reproductive potential due to age truncation associated with reproductive timing, and is not accounted for when using *SSB* as a measure of reproductive potential.

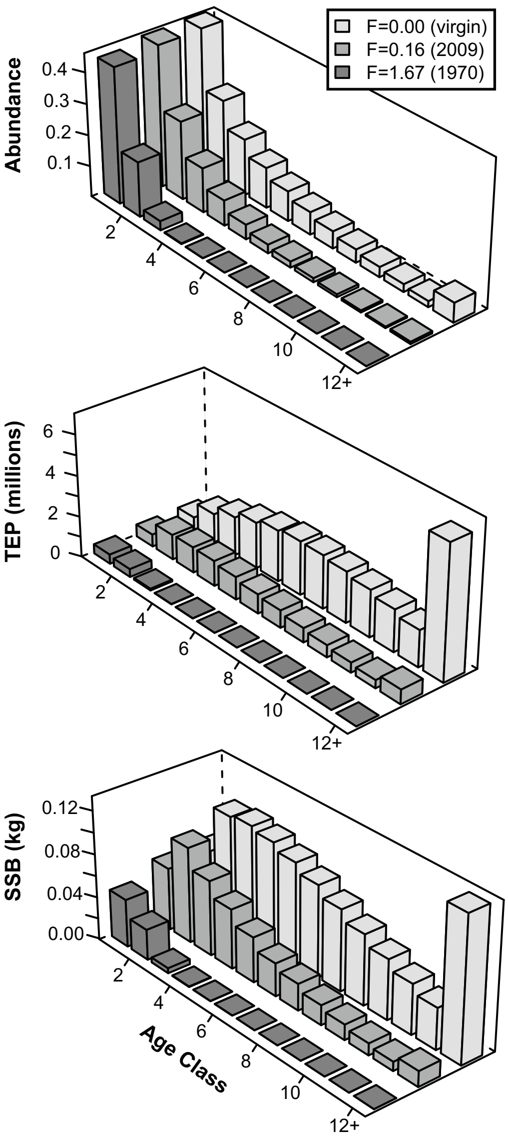

**Fig. 9.** Per recruit abundance, *TEP*, and *SSB* for each age class (*x*-axis) and three fishing pressures (none, low, and high; see legend) at the estimated size-dependent spawning scenario. Note: the sharp increase in *TEP* and *SSB* for the last age class (12+) is due to the accumulation of ages greater than 12 in this plus group under virgin or low fishing pressure years. This occurs in the *SCAM* because a maximum age is not set explicitly in the model, and individuals can survive past twelve years according to an age-specific natural mortality rate (see Section 2).

## 4. Discussion

### 4.1. TEP:SSB relationship

Recent studies have suggested that *TEP* may provide a better measure of *SRP* than *SSB* (Marshall, 2009; Morgan et al., 2009; Mehault et al., 2010; Murua et al., 2010). However, a factor often overlooked is that the ability to estimate *TEP* and its relationship

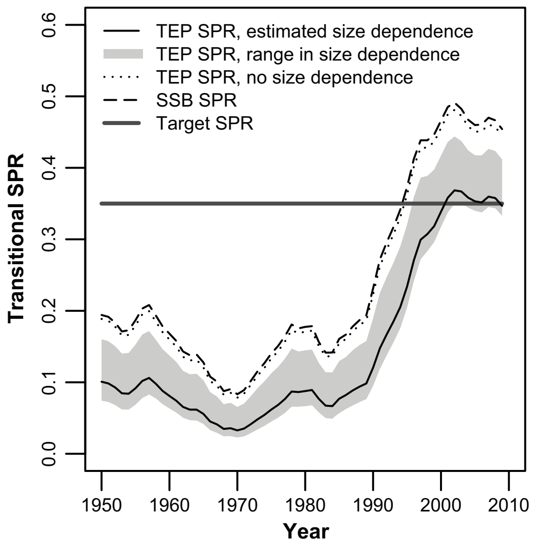

**Fig. 10.** *TEP*- and *SSB*-based spawning potential ratios (*SPR*) from 1950–2009 for the alternative size-dependent spawning scenarios. The thin solid line represents the *SPR* using the estimated size-dependent functional relationship, while the grey shaded areas represent the range in *SPR* estimates due to the confidence range in the size dependence (see Fig. 4b). The *SSB*-based *SPR* estimates varied little (±0.01) among the alternative size-dependent scenarios, so only the average among scenarios is shown.

to *SSB* will vary with a species' reproductive strategy. Although most exploited marine teleosts are highly fecund broadcast spawners (Murua and Saborido-Rey, 2003), they vary in terms of the number of times they spawn within a season (single versus multiple spawning events) and whether their fecundity is determinate (i.e., fixed prior to the beginning of the spawning season) or indeterminate (i.e., they continue to recruit and develop oocytes even after the spawning season has begun; Murua and Saborido-Rey, 2003). The general assumption in fisheries science has been that high fecundity can be achieved only through delayed maturity and greater body size. Although this is appropriate for total spawners, it is not the case for batch spawners with indeterminate fecundity. In these species, annual fecundity is not limited by body cavity size (Lowerre-Barbieri, 2009), and larger, older females have the physiological potential to increase egg production well beyond that predicted from the batch fecundity to size relationship by increasing their spawning frequency (Wright and Trippel, 2009; Lowerre-Barbieri et al., 2011b). This has important implications for the *TEP* to *SSB* relationship, which we modeled by using a suite of size-dependent spawning scenarios. In this study, the "no size dependence" trend mirrored what would be expected in total spawners and species with determinate fecundity, where fecundity is affected by body size but not by spawning frequency. As similarly shown in other studies, we did not find a 1:1 relationship between *TEP* and *SSB*, and the divergence between these two measures of *SRP* greatly increased as the effect of fish size on spawning frequency was incorporated into the analysis (Fig. 11). Importantly, the impact of size-dependence on our estimates of *TEP* was of the same magnitude as differences due to extremes in fishing pressure.

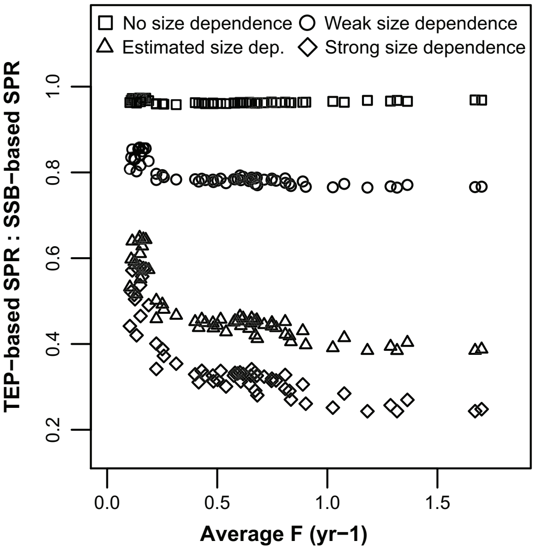

**Fig. 11.** Relationship between the *TEP*- and *SSB*-based *SPR* estimates ($^{\text{TEP-based SPR}}/_{\text{SSB-based SPR}}$). Each data point within a spawning scenario corresponds to the years from 1950 to 2009.

Obtaining accurate estimates of spawning frequency and its relationship with size/age are essential to our ability to accurately estimate *TEP* in species with indeterminate fecundity. However, these data are seldom available, and fish are assumed to have similar spawning seasonality and spawning intervals over the full range of size/age classes. In *C. nebulosus*, first-time spawners often recruit to the spawning population mid-spawning season, and thus can have greatly reduced spawning periods. In addition, older, larger fish demonstrate higher probabilities of spawning, which are not equally distributed throughout the spawning season (Lowerre-Barbieri et al., 2009). To incorporate this level of biological reality into our model, we developed a *GAM* to predict the probability of spawning based on size and date, and an *IBM* to assign when an individual spawned based on whether it was sexually mature and its size on a given date. This allowed us to develop a model with population-based estimates (spawning season of 186 days and spawning interval of 5.6 days) similar to those documented for this species (Brown-Peterson et al., 2002), but demonstrating increased spawning frequency with size and age as has been previously reported for this species (Kupschus, 2004; Roumillat and Brouwer, 2004; Lowerre-Barbieri et al., 2009), as well as other species with indeterminate fecundity (Ganias et al., 2003; Claramunt et al., 2007; Mehault et al., 2010). One weakness of our model, however, is that the *GAM* and resulting estimates of spawning interval were based on the observed spawning fraction of the population, and this can be biased if spatial reproductive behavior exists over a scale not accounted for in sampling (Lowerre-Barbieri et al., 2011b).

### 4.2. Age truncation effects

Age truncation can decrease a stock's resilience (Caddy and Agnew, 2004) and increase its population variability (Anderson et al., 2008), and these effects may be intensified for species with size-dependent reproductive timing. As shown here and in multiple studies, fish size can affect both batch fecundity and spawning frequency in species with indeterminate fecundity (Parrish et al., 1986; Murua et al., 2006; Claramunt et al., 2007; Mehault et al., 2010; Thorsen et al., 2010), causing even small degrees of age truncation to have a large impact on *SRP*. The size of this impact will depend both on the degree of age truncation and the underlying size-dependent relationship with spawning frequency, which is typically unknown and difficult to estimate. In this study, the higher fishing pressure observed in 1970 (average $F = 1.67$) caused the maximum age class to be truncated to age-4, reducing the average age of spawning females from 3.9 (virgin population) to 1.5 years, and decreasing the *TEP* to 3.3% of the virgin population. However, even the low fishing rates in 2009 (average $F = 0.16$) decreased the average spawning age to 2.7 years and the *TEP* to 35% of virgin.

Not surprisingly, the magnitude of this age truncation on reproductive potential was not accurately reflected in abundance or *SSB* values (Fig. 9). For example, at the relatively low fishing pressures in 2009, age classes 6–12 were estimated to contribute between 33–54% of the *TEP* across the range of uncertainty in size dependence, even though they represented less than 5% of the total population abundance. Thus, removal of these age classes through age truncation, even under conditions of relatively weak size dependence, represented a significant decrease in *SRP*, akin to a size-dependent multiplier on the fishing rate. These results are similar to recent literature on other species with indeterminate fecundity, such as tautog *Tautoga onitis* (LaPlante and Schultz, 2007) and southern hake *Merluccius merluccius* (Mehault et al., 2010).

In this study, we focused solely on how age truncation affects reproductive success through increased egg production, but did not address age or size effects on offspring survival (e.g., Berkeley et al., 2004b; Scott et al., 2006; Mehault et al., 2010), or the importance of age composition for dynamic stability of the population (Anderson et al., 2008). Population fluctuations are known to increase as the age composition becomes more juvenescent, resulting from younger age classes tracking environmental fluctuations more readily than older ages, and from changes to demographic parameters that increase nonlinear dynamics (e.g., increased intrinsic growth rates; reviewed in Anderson et al., 2008). Thus, the results presented here are likely conservative with respect to the effects of age truncation, since older age classes not only contribute disproportionately to *TEP*, but may also help stabilize population fluctuations and increase survivorship of progeny, thus improving intergenerational productivity (Berkeley et al., 2004a).

### 4.3. Fisheries management implications

To better integrate the concept of reproductive success into stock assessment procedures, Trippel (1999) introduced the term "stock reproductive potential", defined as the "annual variation in a stock's ability to produce viable eggs and larvae that may eventually recruit to the adult population or fishery." Stock assessments typically assess *SRP* through stock-recruit models or spawning potential ratios (Lowerre-Barbieri, 2009) using *SSB* as a proxy for *SRP* (Murawski et al., 2001). High variability in spawner-recruit data based on *SSB* often masks any potential underlying relationships (Rothschild, 1986; Koslow, 1992; Rose et al., 2001; Marshall et al., 2003), and the results of using more biologically complex measures of *SRP* in stock-recruitment relationships remain equivocal (Morgan et al., 2011). Spawning potential ratios (*SPRs*) were developed to incorporate the stock-recruitment concept without requiring explicit knowledge of the underlying relationship, but require knowledge on the size and age distributions of virgin stocks, as well as the size-dependent relationships with fecundity for these age distributions. Because most assessed stocks have been fished for many years, observed ages are often truncated and historical data are lacking to reflect an unfished state. For example, in the current stock assessment for *C. nebulosus* (Murphy et al., 2011), annual fecundity was estimated for each age class using a POF-based spawning interval (i.e., reciprocal of the proportion with POFs), but due to low sample sizes of older individuals in the dataset, the fecundity estimate used in the assessment was grouped for all age classes greater than five years. Grouping these age classes underestimated the contribution of older individuals and subsequently inflated *SPR* estimates compared to the results of this study, where the size dependence was estimated for older individuals based on the *GAM* fit (Fig. 4b).

Variability in the *SPR* estimates due to uncertainty in the size-dependent spawning relationship was substantial (Fig. 10), and could lead to erroneous perceptions on the status of the stock, particularly when the fishery is near its management target. In this study, the range of uncertainty due to just the size dependence in the *TEP*-based *SPR* encompassed the target level of 35% from 1996–2009 (excluding 2003). Comparatively, if using *SSB* as the *SRP* metric to calculate *SPR*, the stock status would be perceived as healthy since 1995. If *SSB* accurately represents *TEP*, the ratio between the two should remain relatively constant across a range of fishing pressures, but this was not the case in this study (Fig. 11), and in general, using *SSB* to derive *SPR*s underestimates the contribution of older fish (Fig. 10). Discrepancies between *SSB*- and *TEP*-based reference points (Fig. 11) highlights the potential pitfalls in substituting *SSB* as a measure of reproductive potential (Marshall, 2009), particularly when the stock is close to its management target (Murua et al., 2010). Additionally, the inherent individual variability in *SRP* (e.g., due to spatial resource availability) may be compounded by increased population fluctuations when the age composition is truncated (Anderson et al., 2008). Use of precautionary harvest principles could account for this variability, particularly when management targets are set at levels where substantial age truncation occurs. A population's reproductive success may also be derived from a limited set of subpopulations, and the location of these subpopulations can change through time (Berkeley et al., 2004a). Thus, the *SRP* at any given subpopulation can contribute disproportionately to the reproductive success of the broader metapopulation, and protection of both the age and spatial structure may be critical for ensuring that management targets are attainable. Importantly however, perceptions of stock status depend on how the target level is established. If *SSB* is the basis for selecting targets and the procedure to select targets accounts for the appropriate individual- and population-level variability (e.g., through spawner-recruit simulations; Clark, 1993), then *SSB*-based reference points may be suitable for management of a particular stock, even if those reference points do not capture the underlying true reproductive potential. In such cases, differences in perception between *SSB*- and *TEP*-based reference points may not reflect differences in the health of a stock, but inappropriate management targets.

For management of *C. nebulosus* and similar species using *SPRs*, obtaining exact estimates of spawning frequency may not be as critical as characterizing the size-dependent effect on *SRP*. Exploratory analyses with the model (results not presented), where we manually adjusted the intercept of the *GAM* (±1.0, ±2.0) to simulate changes in the average spawning frequency independent of the size dependence, significantly impacted the population *TEP* but had less of an impact on *SPR* estimates relative to the size-dependent effect. Adjusting the intercept by ±1.0 led to a realistic range of potential spawning intervals (3.1–11.6 days average across all age classes; Brown-Peterson et al., 2002), but only impacted the range of *SPRs* by 3.2% averaged across all years (here, for the estimated size-dependent spawning scenario). Adjusting the *GAM* intercept by ±2.0 led to an unrealistically large range of spawning intervals (2.0–23.6 days average across all age classes), but only impacted the *SPR* estimates by 5.9% across all years. Comparatively, the average range in *SPR* estimates due to the statistical uncertainty in the linear size dependence function was 7.9% across all years (Fig. 10). The shape of the size dependence function (e.g., linear versus non-linear) can also influence the *SPR* estimates, depending on the magnitude of difference in the functional shapes. Additional exploratory analyses, where we hypothetically set an asymptotic or declining size-dependent relationship above 550 mm TL (suggested through over-parameterization of the *GAM* at degrees of freedom >5), found variability in the time-averaged *SPR* estimates of 3.3% and 4.7%, respectively, across all years. While these ranges in variability were not as large as those due to the uncertainty in the linear relationship estimated by the *GAM* (mainly due to the bulk of the *TEP* being produced by age classes less than 550 mm TL under some level of exploitation; Fig. 9), these analyses highlight the importance of accurately characterizing the shape of size-dependent relationships across the entire age structure.

Although exact spawning frequency estimates may not be critical for estimating *SPR*, they are important if *TEP* is used in defining stock-recruitment relationships (Wright and Trippel, 2009; Mehault et al., 2010). For some species, parameterizing the stock-recruitment relationship using *TEP* in place of *SSB* may better account for variability in *SRP* and improve the fit of the relationships (Wright and Trippel, 2009; Mehault et al., 2010; Morgan et al., 2011). In addition, using *TEP* in stock-recruitment relationships can provide an alternative gateway to introduce environmental constraints into stock assessment models for ecosystem-based fisheries management (e.g., with extended stock assessment models; Link, 2010), since annual fecundity responds to unique environmental signals (Curtis, 2007; Ganias, 2009).

## 5. Conclusions

This study highlights the importance of size-dependent reproductive timing, its interaction with age truncation, and its consequence on the perception of stock status for management of species with indeterminate fecundity. Under low fishing pressures, we showed that a large portion of a population's annual fecundity was contributed by the oldest individuals. As increased fishing pressures truncated the age structure, reproductive potential declined rapidly, and this decline outpaced concurrent declines in spawning stock biomass. Uncertainty in size-dependent reproductive timing substantially impacted estimates of annual fecundity and stock status, and as the size dependence increased (i.e., longer season duration and shorter spawning intervals as fish grew), *SPR*s declined for any given level of fishing pressure, along with the proportionality between annual fecundity and spawning stock biomass. Although these results are specific for *C. nebulosus*, the general findings of this study should apply to many batch spawners with indeterminate fecundity whose spawning frequency is size or age dependent. In general, as a stock approaches its management target, uncertainty in reproductive potential can bias perceptions of its health, and subsequently trigger inappropriate management actions. Given the impact of size dependence on *SRP*, characterizing these relationships across the full size or age spectrum is critical for assessing reproductive potential when reference points are relative to unexploited conditions. Importantly, these relationships may be non-linear in nature, and use of typical linear models may consequently bias estimates of stock reference points. The techniques presented herein provide a useful mechanism to characterize size-dependent relationships with *SRP* and incorporate these relationships into models to assess stock status for this and similar species with indeterminate fecundity.

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